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Both below-ground and above-ground functional traits can help predict levee grassland root length density as a proxy for flow erosion resistance

Kenny Helsen, Wouter Vannoppen, Olivier Honnay & Jean Poesen

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Helsen, K. (corresponding author, kenny.helsen@ntnu.no)[1,2],
Vannoppen, W. (wouter.vannoppen@kuleuven.be)[3],
Honnay, O. (olivier.honnay@kuleuven.be)[1,*],
Poesen, J. (jean.poesen@kuleuven.be)[3,*]

[1]Plant Conservation and Population Biology, Biology Department, University of Leuven, Kasteelpark Arenberg 31, B-3001, Heverlee, Belgium;
[2]Department of Biology, Norwegian University of Science and Technology, Høgskoleringen 5, 7034, Trondheim, Norway;
[3]Division of Geography and Tourism, Department Earth and Environmental Sciences, University of Leuven, Celestijnenlaan 200E, B-3001, Heverlee, Belgium

*Shared last authorship.

Abstract

Aims: Concentrated flow erosion resistance of herbaceous vegetation is linked to vegetation-level root length density (RLD). However, RLD measurements involve destructive and time-consuming sampling. Since plant species richness, functional diversity and functional composition are expected to affect RLD through either non-additive diversity effects or biomass ratio effects, we evaluated whether these measures can be used as a proxy for RLD in levee grassland communities.

Location: Levee grassland communities, Scheldt estuary, northern Belgium.

Methods: We assessed the strength of correlation between empirically quantified RLD and species richness, functional diversity and functional composition of levee grasslands. More specifically, we used nine below-ground and ten above-ground plant traits retrieved from public databases, and applied linear regressions and partial least square regressions.

Results: Plant functional diversity was a better proxy for RLD than plant species richness, with better predictive performance for below-ground than for above-ground traits. More specifically, the highest predictive power was achieved through integration of functional diversity, functional composition and species richness. This suggests that variation in RLD is driven by a combination of both non-additive diversity effects and biomass ratio effects.

Conclusions: This study provides a first positive indication of the value of plant functional traits retrieved from databases to predict RLD for river levee grasslands. Furthermore, although less reliable than below-ground traits, above-ground traits are still useful for RLD prediction when information on below-ground traits is lacking.

Introduction

Herbaceous vegetation is increasingly recognized as a valuable ecological alternative to civil engineering structures for addressing soil erosion problems (Stokes et al. 2014). This has triggered a plea for more research on the interplay between vegetation properties and soil erosion. Although the direct effects of vegetation cover on splash detachment and inter-rill erosion reduction have been well studied (e.g., Stokes et al. 2014), there is growing evidence that below-ground vegetation biomass is likely more important in reducing (concentrated flow) soil erosion (e.g., Gyssels & Poesen 2003; Gyssels et al. 2005; De Baets & Poesen 2010; Zhang et al. 2013; Berendse et al. 2015). Specifically for concentrated (water) flow erosion, predictive mathematical models, between soil detachment ratio (SDR) and both root length density (RLD) and root mass density (RD) have been proposed to predict the erosion-reducing potential of plant roots (e.g., De Baets & Poesen 2010; Vannoppen et al. 2015). Several studies have subsequently focused on identifying desirable plant species with optimal root parameters (RLD and RD) for soil erosion control

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(e.g., Fattet et al. 2011; Pohl et al. 2011; Burylo et al. 2014). More recently, research has shown that compared to RD, RLD is a much more suitable variable to predict SDR, since it is strongly linked with root architecture (Burylo et al. 2012; Vannoppen et al. 2015).

It has, however, been argued that effective soil erosion reduction management should focus on multispecies or community-level solutions, rather than on single species (Stokes et al. 2014; Zhu et al. 2015). Indeed, next to the direct problems associated with their relatively simple canopy and root structures, monospecific stands are less resistant and resilient to external disturbance or stress events, compared to multispecies communities (Stokes et al. 2014). Recent studies have furthermore shown a large non-additive increase in both RLD and RD with increasing species richness (Sprangers 1999; Mommer et al. 2010; Pérès et al. 2013; Ravenek et al. 2014; Berendse et al. 2015). This non-additive diversity effect can be driven by complementarity, sampling and/or facilitation effects, resulting in vertical segregation of root systems and more efficient exploitation of soil resources (Garnier & Navas 2012; Ravenek et al. 2014; Zhu et al. 2015).

Furthermore, this often observed positive correlation between species richness and root biomass (RLD and RD) suggests that species richness might be used as a proxy for root biomass, and thus (concentrated flow) soil erosion resistance. This presents an appealing shortcut to assess the erosion reducing potential of natural vegetation, since direct measurement of RLD and RD typically involves large workloads and destructive sampling (Lavorel et al. 2007; Garnier & Navas 2012). However, simply relying on species richness as a proxy for root biomass may be incautious (Stokes et al. 2014). Indeed, the insight in the relationship between species richness and root biomass is mainly based on relatively species-poor mesocosm experiments (Mommer et al. 2010; Pérès et al. 2013; Ravenek et al. 2014; Berendse et al. 2015). The question remains whether the positive effect of species richness on erosion reduction remains significant for, often more species-rich, naturally assembled vegetation (Wardle 2016).

In this context, functional trait-based approaches have provided much higher power than species richness-based methods for predicting many ecosystem functions (Mokany et al. 2008; Zhu et al. 2015). This is not surprising, since functional traits are considered more closely linked to both ecosystem functions and services than species identities (Garnier & Navas 2012; Zhu et al. 2015). Likewise, soil erosion resistance in natural systems is likely not only mediated by plant species richness, but also by the functional (root) trait composition of the plant community (Pohl et al. 2009; Ravenek et al. 2014). Indeed, the earlier mentioned non-additive diversity effects might become more pronounced when the species present have contrasting root traits (niche complementarity), since this allows more efficient vertical root segregation (Garnier & Navas 2012; Dias et al. 2013). This would imply a positive relationship between root biomass and community-level *functional diversity* (Díaz et al. 2007; Dias et al. 2013). Additionally, certain root architectural types are known to be more efficient in reducing soil erosion then others (Burylo et al. 2014). The biomass ratio hypothesis postulates that differences in the abundance of species exhibiting these 'efficient' root types will proportionally affect community-level soil erosion resistance, independent of species richness (Grime 1998). This hypothesis suggests significant relationships between root biomass and community-level measures of *functional composition* (Díaz et al. 2007; Dias et al. 2013). An additional advantage of a functional trait framework is that it allows generalization across communities with different species pools (Burylo et al. 2014). The limited number of studies that have explored the importance of functional community characteristics have already shown that both functional composition (Zhu et al. 2015) and functional diversity (Martin et al. 2010; Ravenek et al. 2014; Zhu et al. 2015) in root traits can help predict soil erosion resistance, independently of species richness.

Functional root traits tend to cluster in specific trait syndromes across life history strategies (the root economics spectrum; Roumet et al. 2006; Prieto et al. 2015). These syndromes suggest that valuable functional information can be obtained by evaluating a limited number of functional root traits. More interestingly, these root traits have, in certain cases, been linked with above-ground (leaf, stem) functional traits at both the species level (Reich 2014; Cheng et al. 2015) and the community level (Reich 2014; Prieto et al. 2015). This suggests that using easy to measure above-ground functional traits might provide sufficient information to reliably predict plant community-level below-ground biomass (RLD and RD), and thus erosion reducing potential (Craine et al. 2001; Lavorel et al. 2007; Garnier & Navas 2012). Several other studies have, however, failed to show a close correlation between above-ground and below-ground traits (Tjoelker et al. 2005; Freschet et al. 2015). This approach nonetheless remains worth exploring, since, unlike root traits, many above-ground functional traits have been assembled for a wide range of species in public databases [e.g., LEDA and TRY; Kleyer et al. 2008; Kattge et al. 2011)], thus circumventing potential time-consuming and destructive sampling to assess community-level RLD.

In this study, we evaluated whether species richness, functional diversity and functional composition of a set of above-ground and below-ground plant traits can predict RLD for grassland vegetation plots on the river levees along

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the Scheldt estuary in Belgium, which are prone to wave overtopping events. The studied grasslands span a representative range in species richness, typical for levee grassland communities (6–30 species per 2 m × 2 m plot). We directly measured RLD from collected soil samples, and extracted functional above-ground and below-ground traits from online databases. This setup allowed us to evaluate the following research questions: (1) can plant species richness, plant functional diversity and plant functional composition independently explain variation in RLD, and which variables have the highest predictive power; (2) are root functional traits extracted from general trait databases accurate enough to explain variation in RLD; and (3) are above-ground functional traits a reliable alternative for root functional traits in predicting RLD?

Methods

Study area and sample collection

The study was performed on the levees along the Durme and Scheldt rivers of the Scheldt estuary in northern Belgium (Fig. 1). A relatively large soil volume of 24 000 cm^3 of the 0–0.15 m topsoil was collected for 15 locations in Jul 2012 using a 0.40 m × 0.40 m metal frame (Fig. 1). Soil samples were washed in the lab to separate plant roots from the soil. Total length of all roots with a diameter >1 mm was directly measured from these samples. For smaller roots, specific root length ($m \cdot kg^{-1}$) was calculated from 200 roots and subsequently used to estimate the total root length from their mass. The plot-level RLD, i.e. the total root length per soil volume (RLD, $km \cdot m^{-3}$) was obtained by dividing the total root length by the soil volume (0.024 m^3). Only the topsoil up to 0.15 m below the surface was considered, since concentrated flow erosion reduction is mainly driven by RLD patterns in the topsoil (De Baets & Poesen 2010; Vannoppen et al. 2015). The vegetation composition (% cover of all tracheophytes) of these 15 locations was surveyed using two 2 m × 2 m plots for each RLD sampling location. Since RLD sampling had been destructive for the vegetation, plots were positioned on both sides of the original RLD sampling location. Vegetation sampling was performed twice for each location, at the end of Jul 2014, and at the end of Aug 2014. For final analysis, both vegetation plots were averaged, resulting in data for 15 vegetation plots (see Appendix S1 for the final vegetation matrix).

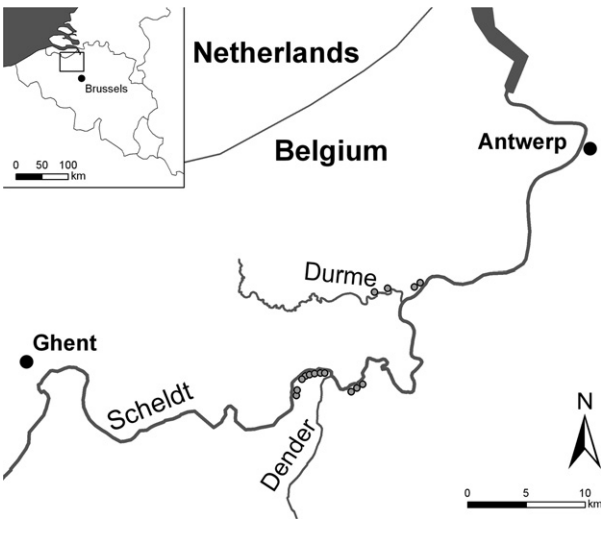

Figure 1. Location of the 15 vegetation plots (open circles) on the Durme and Scheldt river levees.

Plant traits and functional composition

Nineteen functional plant traits were selected for their expected relevance to RLD (Appendix S2). This selection consisted of nine below-ground (root) traits that are expected to be important for soil erosion reduction, namely root:shoot ratio (RSR), root dry mass (RDM), root architecture (adventitious, fibrous and taproot presence), epigeogenous rhizome presence, hypogeogenous rhizome presence and horizontal stem presence (Stokes et al. 2009, 2014). The selection furthermore consisted of ten above-ground traits that are related to a species growth and competition strategy, namely relative growth rate (RGR), specific stem density (SSD), leaf size, leaf longevity, life span, seed longevity and seed number. We also included the above-ground traits related to the three main functional dimensions; namely resource use (specific leaf area; SLA), competitive ability (plant height) and dispersal ability (seed mass) (Garnier & Navas 2012). Although RSR and horizontal stem presence are strictly not 'below-ground' traits, we nonetheless believe that both are strongly linked to root effects. Trait values were extracted from several online databases (Klotz et al. 2002; Kleyer et al. 2008; Klimešová & de Bello 2009; Kattge et al. 2011; Hempel et al. 2013). The seed longevity index was calculated according to Thompson et al. (1997) and Bekker et al. (1998). The traits leaf size, plant height and seed number were logarithmically transformed prior to further analyses to reduce the influence of extreme values. Although for RSR, RDM, SSD and fibrous root presence, trait values were available for a relatively low number of species (<50%), the missing values almost exclusively concerned less common species with low abundances (Appendix S2).

Each plot was subsequently described in terms of the abundance-weighted average value of each trait across all species present in the plot (community-weighted trait means, CWM) for the functional composition analysis (Díaz et al. 2007). CWM calculations were performed in FDiversity (Casanoves et al. 2011).

Taxonomic and functional diversity

We calculated three measures of taxonomic diversity: species richness (S), Simpson diversity (D) and Shannon evenness (E). Additionally, we calculated four measures of functional diversity, together addressing all three independent components of functional diversity. These components consist of the amount of filled trait space (functional richness), the regularity of the distribution of abundance in trait space (functional evenness), and the spread in distribution of abundance within trait space (functional divergence) (Mason et al. 2005; Garnier & Navas 2012). Functional richness was quantified with FDc and wFDc (Petchey & Gaston 2006). wFDc is an extension of FDc, taking into account species relative abundances. FDc and wFDc calculations were based on Gower dissimilarity matrices, with dendrogram construction based on the linkage algorithm of Ward (1963). We preferred the use of FDc and wFDc above the FRic of Villéger et al. (2008), since FRic calculation requires strong data dimensionality reduction. Functional evenness and functional divergence were, respectively, quantified with FEve and FDiv (Villéger et al. 2008). Before calculation of functional diversity, all traits were standardized and missing trait values were replaced by the CWM for the given trait in the given vegetation plot. All four functional diversity measures were calculated twice, once for all below-ground traits combined and once for all above-ground traits combined, with the program FDiversity (Casanoves et al. 2011).

Statistical analysis

We used several statistical analyses to examine the relationships between RLD (response variable) and species diversity, functional diversity and functional trait composition (predictors). RLD was correlated with species and functional diversity using simple linear regression in SPSS 20.0 (SPSS, Chicago, IL, US). FEve for both the above-ground and below-ground traits and FDiv for the below-ground traits were x^3-transformed to obtain independence of residuals. To assess the predictive power of the community trait composition on RLD, while taking into account trait intercorrelations (collinearity; Appendix S3), we adopted a partial least squares regression approach (PLS; Haenlein & Kaplan 2004). Although not commonly applied in ecological studies, PLS has been shown to produce superior results compared to more common indirect gradient analyses (Carrascal et al. 2009). PLS is a variance-based structural equation modelling technique, focussing on maximizing the variance of the response variable explained by the predictors (Haenlein & Kaplan 2004). More specifically, the technique reduces the number of variables by constructing a few components, while at the same time maximizing their covariance with the response variable. The optimal number of components is evaluated using leave-one-out cross-validation, simultaneously resulting in both a root mean-square error estimate (RMSE) and the cross-validated R^2 (Q^2), both expressing the predictive power of the model. PLS is considered specifically fit for analysing data sets with many, strongly intercorrelated predictors and small sample sizes (Haenlein & Kaplan 2004). We performed two PLS regressions based on (1) all below-ground functional trait CWMs; and (2) all above-ground functional trait CWMs. Both models were reduced by eliminating predictors with low variance influence on the PLS projections (VIP < 0.80; Chong & Jun 2005) and are henceforth referred to as 'traits PLS model'.

We furthermore constructed two 'full' PLS models, one based on the below-ground traits and one based on the above-ground traits, to evaluate how the different measures of functional diversity, species diversity and functional composition (CWMs) together help predict variation in RLD. Additionally, we constructed two 'diversity' PLS models, based on only species and functional diversity measures, one for below-ground traits and one for above-ground traits. All four models were reduced by eliminating predictors with a VIP < 0.80. All PLS regressions were performed with XLSTAT (Addinsoft, New York, NY, US), on the standardized (z-transformed) data (both response variable and predictors), thus resulting in standardized coefficients as model output.

Results

Our data span a wide range in both RLD (6.9–133.0 $km \cdot m^{-3}$) and species richness (6–30 species; Appendix S1). Species richness ($F = 12.8$, $P = 0.003$), and to a lesser extent Simpson diversity ($F = 6.1$, $P = 0.028$), were positively correlated with RLD (Fig. 2a, Appendix S4). All functional diversity measures based on below-ground traits were positively correlated with RLD (FDc: $F = 16.2$, $P = 0.001$, wFDc: $F = 12.0$, $P = 0.004$, FEve: $F = 12.5$, $P = 0.004$ and FDiv: $F = 12.3$, $P = 0.004$; Fig. 2b–d, Appendix S4). For functional diversity of above-ground traits, however, only FDc ($F = 15.7$, $P = 0.002$) and wFDc ($F = 13.1$, $P = 0.003$) were significantly, positively correlated with RLD (Fig. 2b, Appendix S4). Functional diversity of below-ground traits explained relatively high variation (R^2 FDc = 0.521), closely followed by functional diversity of above-ground traits (R^2 FDc = 0.513), with species richness explaining less variation (R^2 $S = 0.457$). The diversity PLS models showed that combined species and functional diversity predicted relatively high amounts of RLD variation based on both below-ground traits ($R^2 = 0.732$, $Q^2 = 0.617$) and above-ground traits ($R^2 = 0.625$, $Q^2 = 0.522$; Appendix S5).

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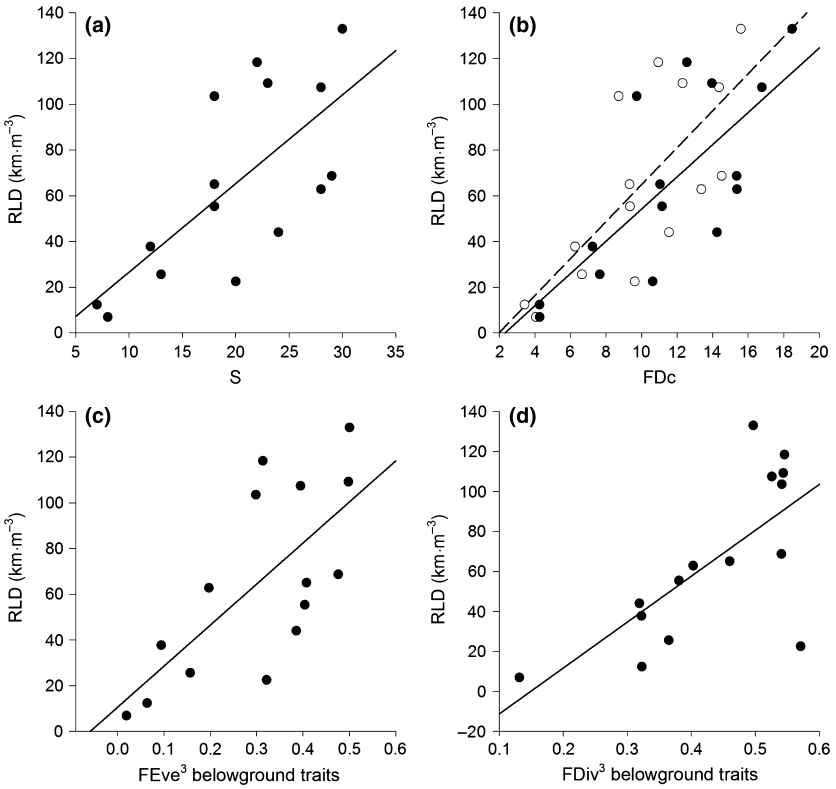

Figure 2. Relationships between root length density (RLD) and species richness and functional diversity. Regression lines for: (**a**) species richness (*S*), (**b**) Petchy and Gaston's functional diversity (FDc) for above-ground traits (open circles, dotted line) and below-ground traits (full circles, continuous line), (**c**) x^3-transformed functional evenness of below-ground traits (FEve) and (**d**) x^3-transformed functional divergence of below-ground traits (FDiv).

The final (reduced) traits PLS models showed a subset of both below-ground and above-ground traits that explain a relatively high percentage of variation in RLD (respectively $R^2 = 0.591$, $R^2 = 0.619$; Tables 1 and 2). The predictive power of these models, tested through cross-validation, was nonetheless somewhat lower than their R^2 values suggest (respectively $Q^2 = 0.427$, $Q^2 = 0.473$). For both below-ground and above-ground traits, a two-component PLS model could most reliably predict RLD. For below-ground traits, the first component was most strongly correlated with hypogeogenous rhizome presence (−), adventitious root presence (−), taproot presence (+), RDM (+) and RSR (+) (Table 1, Fig. 3a). The second component was mainly driven by differences in horizontal stem presence (−). Fibrous root presence, epigeogenous rhizome presence and mycorrhizal frequency, on the other hand, did not provide a good predictive ability for RLD (VIP < 0.80). For above-ground traits, the first component was mainly explained by variation in plant height (−), life span (−), leaf size (−) and leaf longevity (+), while the second component was mainly driven by additional variation in leaf size (−) and plant height (−) (Table 2, Fig. 3b). None of the seed-related traits, nor SLA, SSD or RGR was important in explaining variation in RLD (VIP < 0.80).

The final full (reduced) PLS model consisted of two PLS components for both below-ground and above-ground traits. Most variables were strongly correlated for both models, resulting in a high proportion of the total variation of the predictor data set explained by the first PLS component (below-ground traits: 79.5%, above-ground traits: 72.3%). These models resulted in an R^2 of 0.816 for below-ground traits and 0.699 for above-ground traits (Tables 1 and 2), and a Q^2 (predictive power) of, respectively, 0.635 and 0.564 (Tables 1 and 2). The full PLS models were consistent with the results of the linear regressions and traits PLS models. For below-ground traits, the first component was most strongly linked with species richness, all functional diversity measures and four functional traits. The second component was mainly driven by variation in Shannon evenness, FDiv and horizontal stem presence (Table 1, Fig. 3a). For above-ground traits, the first component was chiefly linked to species richness, FDc, wFDc and four functional traits. The second component was most strongly related to Shannon evenness, leaf size and seed number (Table 2, Fig. 3b).

Table 1. Results of the PLS models on root length density (RLD), based on below-ground functional traits.

	Traits PLS Model		Full PLS Model	
	Weights	Coefficients	Weights	Coefficients
S			0.308/0.131	0.156
D			0.248/−0.225	−0.090
E			0.148/−0.583	−0.346
FDc			0.326/0.200	0.205
wFDc			0.303/0.063	0.111
FEve*			0.306/0.118	0.148
FDiv*			0.305/0.496	0.394
RSR	0.403/−0.122	0.064	0.267/−0.033	0.040
RDM	0.482/0.424	0.365	0.318/0.246	0.234
Adventitious Roots	−0.457/−0.327	−0.309	−0.302/−0.124	−0.150
Taproot	0.438/0.144	0.210	0.290/0.036	0.090
Hypogeogenous Rhizome	−0.407/0.124	−0.064	−0.269/0.112	−0.011
Horizontal Stem	0.195/−0.828	−0.359	0.129/−0.485	−0.287
N	2		2	
R^2	0.591		0.816	
Q^2	0.427		0.635	
RMSE	25.320		16.996	

Results given for both the (reduced) traits PLS model and the (reduced) full PLS model. Modified weights (loadings) on each PLS component and standardized coefficients given for each predictor. Number of PLS components (*N*), full model R^2 and cross-validation results (Q^2 and RMSE) given for each model. *S*, species richness; *D*, Simpson diversity; *E*, Shannon evenness; FDc, Petchy and Gaston's functional diversity; wFDc, abundance-weighted FDc; FEve, functional evenness; FDiv, functional divergence.
*x^3 transformation.

Table 2. Results of the PLS models on root length density (RLD) based on above-ground functional traits.

	Traits PLS Model		Full PLS Model	
	Weights	Coefficients	Weights	Coefficients
S			0.378/0.158	0.161
D			0.304/−0.101	0.049
E			0.182/−0.444	−0.107
FDc			0.397/0.202	0.182
wFDc			0.380/0.124	0.149
Plant Height*	−0.532/−0.198	−0.321	−0.341/−0.035	−0.107
Leaf Size*	−0.507/−0.813	−0.555	−0.325/−0.743	−0.354
Leaf Longevity	0.480/−0.527	0.007	0.308/0.059	0.106
Life Span	−0.479/0.219	−0.130	−0.307/0.017	−0.079
Seed Number*			−0.139/0.480	0.132
N	2		2	
R^2	0.619		0.699	
Q^2	0.473		0.564	
RMSE	24.423		21.708	

Results given for both the (reduced) traits PLS model and the (reduced) full PLS model. Modified weights (loadings) on each PLS component, coefficients given for each predictor. Number of PLS components (*N*), full model R^2 and cross-validation results (Q^2 and RMSE) given for each model. *S*, species richness; *D*, Simpson diversity; *E*, Shannon evenness; FDc, Petchy and Gaston's functional diversity; wFDc, abundance-weighted FDc.
*Logarithmic transformation.

Discussion

Taxonomic diversity

This study adds to the growing body of literature demonstrating a positive relation between species richness and RLD (e.g., Sprangers 1999; Mommer et al. 2010; Berendse et al. 2015), and thus underlines the potential of species-rich communities to tackle concentrated flow erosion problems (Stokes et al. 2014; Berendse et al. 2015). The predictive power of taxonomic diversity seemed to be mainly based on the actual number of species (45.7% variation explained), rather than on differences in their abundances. However, species evenness did significantly contribute to the second component of full PLS model,

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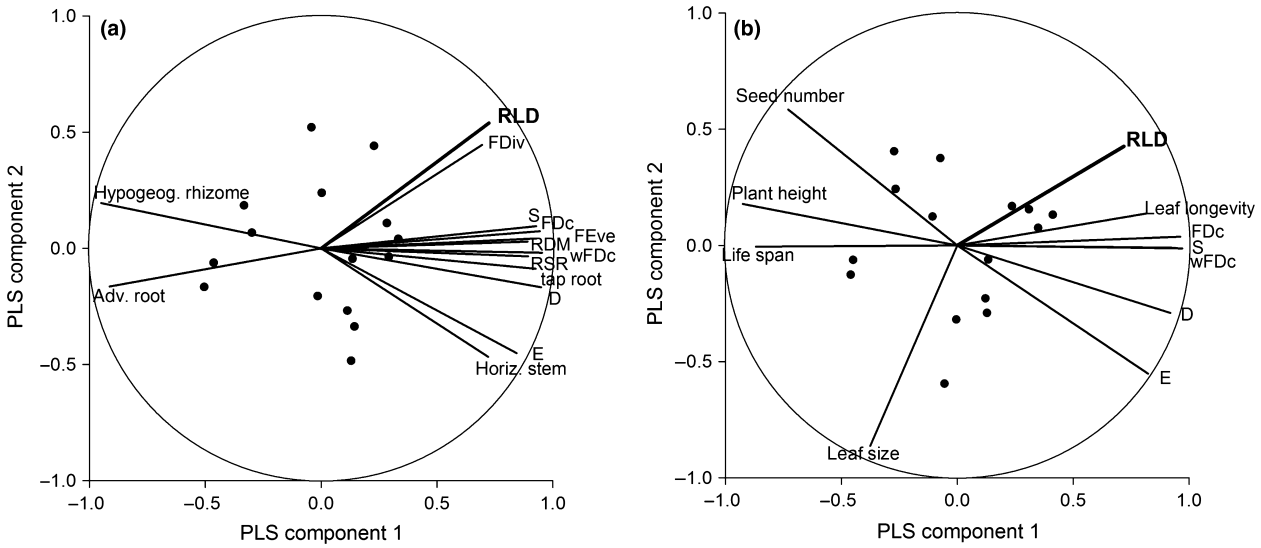

Figure 3. Projection of standardized response variable (root length density, RLD), predictors and vegetation plots against the two PLS components for: (**a**) the full PLS model for below-ground traits, and (**b**) the full PLS model for above-ground traits. Vegetation plots as points, predictors and response as vectors. For explanation of plant traits, see Appendix S2. *S*, species richness; *D*, Simpson diversity; *E*, Shannon evenness; FDc, Petchy and Gaston's functional diversity; wFDc, abundance-weighted FDc.

suggesting that differences in evenness provide additional predictive power for RLD, independent of species richness.

Below-ground traits

All three components of functional diversity based on below-ground functional traits can contribute to predicting RLD variation in our study. Functional richness (FDc) has a higher predictive power than species richness (Garnier & Navas 2012). This seems to suggest that the non-additive diversity effect on RLD in species-rich communities is better explained by the richness in functional root traits than by species richness, supporting the view that niche-based processes are driving these patterns (niche complementarity; Martin et al. 2010; Ravenek et al. 2014; Zhu et al. 2015). Further research should, however, try to disentangle the effects of species richness and functional richness on RLD to assess the validity of this result, possibly with the use of null models. Nonetheless, the niche complementarity hypothesis is further supported for our data by the additional predictive power of functional divergence (on the second PLS component), next to the variation predicted by functional richness (on the first PLS component) in the full PLS model. Similarly to taxonomic diversity patterns, RLD is mainly governed by the presence of a high number of functional root trait syndromes rather than by differences in abundance of these types (slightly lower R^2 for wFDc). Although functional evenness is theoretically expected to be independent of species richness (Mason et al. 2005; Villéger et al. 2008), in our study, FEve co-varied with species richness, suggesting that its inclusion in the full PLS model is likely due to its collinearity with species/functional richness (Appendix S3).

Community-level below-ground trait composition was also related to differences in RLD. More specifically, our results confirm that the previously shown positive relation between RLD, and RSR and root dry matter content at the species level, persist at the community level (CWMs; Gyssels et al. 2005; Fattet et al. 2011; Stokes et al. 2014). Although we had relatively low coverage for both of these traits, we believe that the observed trait patterns reflect true community patterns, since missing values almost exclusively concerned low abundance species that have limited effect on CWM calculations. This nonetheless illustrates the limited coverage of below-ground traits in public databases (e.g., Kleyer et al. 2008; Kattge et al. 2011). Further studies on more extensive data sets using field-measured trait values should be performed to evaluate the possible bias of missing values on the observed patterns. The negative effect of (shallow) hypogeogenous rhizomes, horizontal stems and adventitious roots on RLD also concurs with the literature (Genet et al. 2010), and is likely caused by the dominance of competitive rhizomatous species in the species-poor plots (e.g., *Eupatorium cannabinum*, *Lamium album*, *Urtica dioica*). However, we did not observe the persistence of all species-level trait patterns during upscaling. Indeed, the negative relation between RLD and taproot presence at species level (De Baets & Poesen 2010; Burylo et al. 2014) was reversed at the community level. This counterintuitive result is likely caused by an absence

of species with taproot systems in species-poor, low RLD grasslands plots in our study. The absence of strong predictive power for fibrous root presence and mycorrhizal frequency was also unexpected (Burylo et al. 2014; Stokes et al. 2014).

Although the diversity PLS model explained more variation in RLD than the traits PLS model, trait CWMs and functional diversity measures were partly inter-correlated. However, it is impossible to separate the causal effects of either trait CWMs or functional diversity on RLD in our data set (Dias et al. 2013). The full PLS model nonetheless clearly indicated that both trait CWMs and functional diversity measures combined allow for a much better predictive model. This shows that both biomass ratio effects and non-additive diversity effects are together driving RLD patterns across plots (Grime 1998; Díaz et al. 2007; Dias et al. 2013). This is in accordance with the results of Zhu et al. (2015) for semi-arid grasslands in China. Our full PLS model more specifically resulted in quite high predictive power over RLD (R^2 = 81.6%, Q^2 = 63.5%). Since our study was performed on a rather limited number of data points, we encourage others to evaluate the validity of our predictive model using the provided standardized coefficients on more extensive data sets, for other vegetation systems (Table 1).

Above-ground traits

For above-ground traits, only the functional richness component of functional diversity was significantly correlated with RLD, with a somewhat lower predictive power than that for functional diversity of below-ground traits. The goodness-of-fit of functional richness of above-ground trait was nevertheless still higher than that of species richness, suggesting that the non-additive diversity effect is likely still more closely linked to above-ground trait composition than to species richness (Garnier & Navas 2012). This suggests that, at least some, functional above-ground traits are relatively closely linked to functional root traits that are relevant for RLD variation.

Interestingly, none of the reproductive traits (other than seed number), or SLA was retained in the final models. This suggests that root traits (and thus RLD) cannot be reliably predicted by traits related to the dispersal ability or resource-use trait axes (Garnier & Navas 2012). The CWMs of several other above-ground traits (plant height, leaf size, leaf longevity and life span) nonetheless co-varied with RLD. This indicates that mainly traits related to competitive ability present relatively useful proxies for RLD prediction. However, a larger-scale evaluation of potential (competition-related) above-ground traits might provide more traits of high predictive value.

Similarly to the results on below-ground traits, the diversity PLS model had a slightly higher predictive power than the traits PLS model. Nonetheless, the full PLS model again confirmed that both biomass ratio effects (CWMs) and non-additive diversity effects (functional diversity) shape RLD variation and, more importantly, that both of these processes are partly captured by above-ground functional traits. Although lower than the predictive power of the full PLS model based on below-ground traits, the full PLS model on above-ground traits nonetheless explained a substantial portion of the variation in RLD (R^2 = 69.9%, Q^2 = 56.4%), demonstrating its usefulness when information on below-ground traits is lacking (Lavorel et al. 2007; Stokes et al. 2014). Again, this model should be validated for larger data samples, using the provided standardized coefficients (Table 2).

In conclusion, this study provides a first positive indication that above-ground functional traits can provide a surrogate for below-ground traits to predict RLD, and in extension, possibly, SDR for natural grassland communities. More specifically, using above-ground traits, we can simultaneously quantify non-additive diversity and biomass ratio effects with the help of both functional diversity and functional composition (CWM) measures. However, larger-scale evaluation and validation of these results should be performed in different vegetation types to allow a more detailed evaluation of the potential value of this framework.

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Author contribution

K.H. performed statistical analyses and drafted the manuscript; W.V. performed study site selection and fieldwork; O.H. and J.P. participated in the design of the study and helped to draft the manuscript. All authors read and approved the final manuscript. O.H. and J.P. are shared last authors for this manuscript.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Final plot x species data matrix.

Appendix S2. Overview of the selected functional traits.

Appendix S3. Correlation matrix for all predictor variables.

Appendix S4. Linear regressions results between root RLD and diversity measures.

Appendix S5. Results of the diversity PLS models on root length density.

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Graphical Abstract

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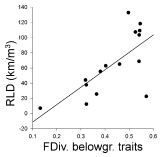

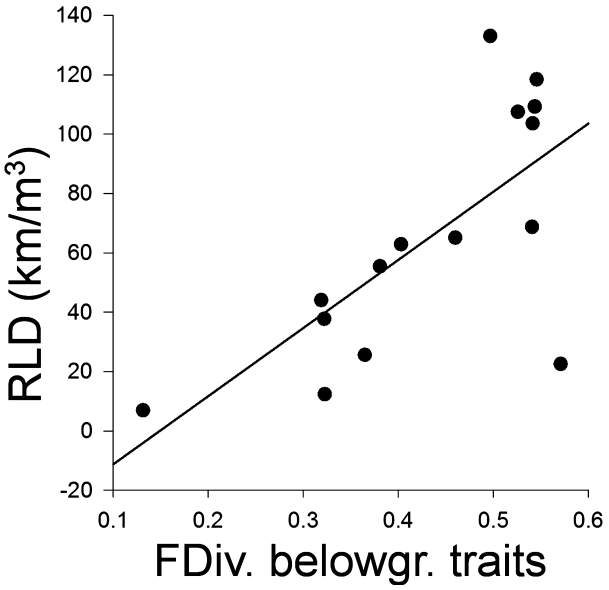

We show that vegetation-level root length density (RLD), a proxy for flow erosion resistance, is correlated with functional diversity and functional composition, likely through non-additive diversity effects and biomass-ratio effects. This illustrates that database collected functional trait values can be used to predict RLD variation for levee grasslands, possibly presenting a non-destructive alternative to assess grassland erosion resistance.